[From the American Journal of Science, Vol. XLVIII, July, 1894.]

FOOTPRINTS OF VERTEBRATES IN THE COAL MEASURES OF KANSAS.

WITH PLATES II AND III.

THE TYPICAL ORNITHOPODA OF THE AMERICAN JURASSIC.

WITH PLATES IV–VII.

By O. C. Marsh.

[From the American Journal of Science, Vol. XLVIII, July, 1894.]

Art. X.—*Footprints of Vertebrates in the Coal Measures of Kansas;* by O. C. Marsh. (With Plates II and III.)

The Museum of Yale University contains a small collection of footprints of much interest, which were found in 1873, in the Middle Coal Measures, near Osage, in southeastern Kansas. This collection is part of a larger series of specimens obtained at the locality by the late Prof. B. F. Mudge, who published a short notice of the discovery, which was subsequently copied in this Journal (vol. vi, p. 228, 1873). The writer examined this entire collection at Manhattan, Kansas, in the autumn of 1873, and secured it for the Yale Museum. The more important specimens were then sent to New Haven, and tracings and notes were taken of the others, which were left to be forwarded later. A careful re-examination of these footprints has been recently made by the writer, and the main results are given in the present article.

The impressions are well preserved in a calcareous shale, which separates readily into thin slabs, each representing a surface of the beach at the time the footprints were made upon it. A few shells in the shale are sufficient to prove that the formation is marine. Trails of annelids, and perhaps of other invertebrates, are seen on some of the surfaces. The footprints of vertebrate animals, however, are of paramount importance, and the large number and variety of these here recorded on a single surface, if they could be rightly interpreted, would form an interesting chapter of land vertebrate life in the Carboniferous, about which so little is at present known.

On Plate II, accompanying the present article, five distinct series of footprints are shown, each one-twelfth natural size. All were found on essentially the same surface, and at one locality. The five different animals they represent were thus contemporaries, and indicate a wealth of air-breathing, land vertebrate life at this period, hitherto unsuspected.

With these impressions were still others, made either by animals nearly allied or by the same animals under different circumstances. These need not be further noticed in this connection, but they serve to emphasize the diversity of life at this point. The typical series are briefly described below.

Nanopus caudatus, gen. et sp. nov.

The first series represented on Plate II, figure 1, indicates the smallest animal that here left a distinct series of footsteps, and the only one in which an imprint made by the tail was preserved. This small quadruped had evidently but three functional toes on the fore feet and four on those behind. The fore feet were considerably smaller than the hind feet. The impressions made by the latter are nearly all separate from the anterior footprints, although at times slightly overlapping them. One fore and one hind footprint of this series are represented, natural size, on Plate III, figure 1.

The nature of the animal indicated by these impressions can at present be a matter of conjecture only, but the probabilities are in favor of its reference to the Amphibians rather than to the true *Reptilia*. As it is evidently distinct from anything hitherto described, the above name is proposed for it.

Limnopus vagus, gen. et sp. nov.

In figure 2, Plate II, a second series of footprints is represented, somewhat larger than those above described, and evidently made by a very different animal. A fore and hind footprint of this series are shown, natural size, in figure 2, Plate III. The front feet had four functional toes, while those behind had five, all well developed. The impressions of the hind feet, as a rule, overlap those of the corresponding fore feet. No indications of a tail can be detected. In length of stride, and in the distance between the footsteps of the right and left sides, the present series is proportionately about the same as those above described, although the animals differed much in size. They were probably both Amphibians, and may have been nearly allied.

Dromopus agilis, gen. et sp. nov.

The third series of footprints shown on Plate II, figure 3, is of special interest, and indicates an animal very distinct from the two already described. On Plate III, figure 3, an outline impression is given, natural size, of one double footmark of this series, made by the fore and hind feet of the left side. This diagram represents the impression of the phalanges sufficiently in detail to indicate their number and general form. A striking feature in the fore and hind feet of this animal was

the long, slender digits, terminated by sharp claws. Another point of interest, as recorded in the footprints, is that the animal in walking swung the hind feet outward, and so near the ground that the ends of the longer toes sometimes made trails in the mud, marking accurately the sweep of the foot. This would seem to indicate a comparatively short hind leg, rather than the long, slender one which the footmarks themselves naturally suggest.

The animal that made these interesting footprints was probably a Lacertilian rather than an Amphibian, but there is also a possibility that it was a primitive Dinosaur.

Allopus littoralis, gen. et sp. nov.

Besides the footprints above described, which pertain to animals of comparatively small size, there are several other series in this collection made by very large animals, which were probably all Labyrinthodonts. These tracks were made on the same beach, and at about the same time as the small footprints, but not all under the same circumstances. The largest animal thus represented appears to have walked on one part of the beach that was quite firm, leaving very shallow footprints, and again to have traversed another part, quite near the first, but slightly covered with water, or at all events so soft that deep impressions were made by the feet, while the toes of the hind feet also left deep trails as they swung outward at each step. On Plate II, figures 4 and 4a, these two kinds of footprints are represented. They show the stride of the animal, and, as put together, also denote the width between the footprints of the two sides, so that the series can be compared with the others on the same plate.

These tracks show that the animal had five toes in the fore feet and four behind. The hind feet show a distinct impression of a sole. There is no imprint of a tail, even where the mud appears to have been deep.

Baropus lentus, gen. et sp. nov.

The most abundant of the large footprints are represented by several series, which are remarkably uniform in stride and in width between the right and left rows. One of these series is represented on Plate II, figure 5, and this is typical of the others. The animal that made these footprints evidently had four functional toes in front and the same number behind. On the inner side of each foot, however, there was a projection, which, in the hind feet, was quite prominent and characteristic, but can hardly be interpreted as the imprint of the first digit. Nearly all these footprints show a distinct impression of a sole. This is usually faint in the tracks of the fore feet, but strongly marked in those behind.

It is hardly necessary at this time to attempt a detailed comparison of the footprints above described with those already on record, but the writer hopes to do this later. The present specimens all have well-marked characters, and, being from a single horizon and locality, have a value of their own as throwing light on the land vertebrate life, during the deposition of the true Coal Measures. If, in themselves, they add but little to what is already known, they at least offer encouragement to investigators in an interesting field not yet systematically explored. The publications of Logan, Lyell, King, Lea, Dawson, and others, have already made known discoveries of importance in this country, and others have been recorded in the Old World.

So far as at present known, land vertebrate life began in the Carboniferous age, no footprints or other remains of this kind having been detected below the Subcarboniferous. That such remains will eventually be found in the Devonian, there can be no reasonable doubt, and perhaps even in the Silurian, if the land surfaces then existing can be explored.

Yale University Museum, New Haven, Conn., June 12, 1894.

EXPLANATION OF PLATES.

Plate II.

Figure 1.—Series of footprints of *Nanopus caudatus*, Marsh; showing, also, impression made by the tail.

Figure 2.—Series of footprints of *Limnopus vagus*, Marsh.

Figure 3.—Series of footprints of *Dromopus agilis*, Marsh; showing trails made by the toes.

Figure 4.—Two pairs of footprints of *Allopus littoralis*, Marsh; right side.

Figure 4a.—Footprints of same; showing trails made by the toes; left side.

Figure 5.—Series of footprints of *Baropus lentus*, Marsh.

All the figures are one-twelfth natural size.

Plate III.

Figure 1.—Outline of left fore and hind footprints of *Nanopus caudatus*.

Figure 2.—Outline of left fore and hind footprints of *Limnopus vagus*.

Figure 3.—Diagram of left fore and hind footprints of *Dromopus agilis*.

All the figures are natural size.

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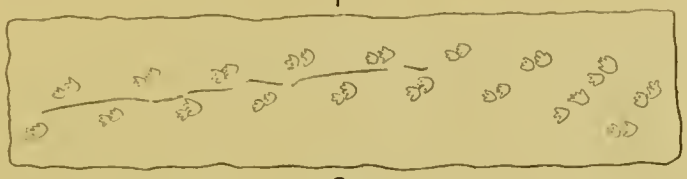

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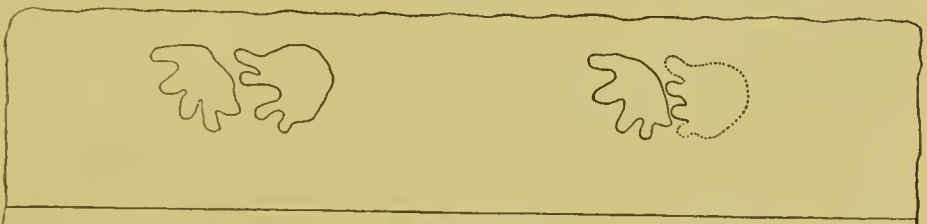

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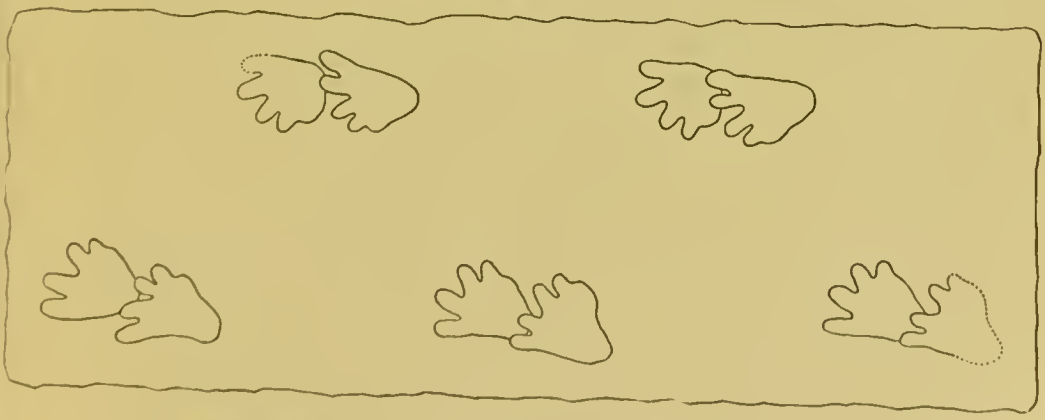

FOOTPRINTS FROM KANSAS COAL MEASURES. One-twelfth natural size.

FOOTPRINTS FROM KANSAS COAL MEASURES. Natural size.

ART. XI. — *The Typical* ORNITHOPODA *of the American Jurassic;* by O. C. MARSH. (With Plates IV–VII.)

THE herbivorous Dinosaurs now known from the Jurassic deposits of this country consist mainly of the gigantic *Sauropoda* and the huge *Stegosauria*, both quadrupedal forms. A third group is the bipedal *Ornithopoda*, which contains the genus *Camptosaurus* as well as various smaller and more bird-like types. The first two groups have been investigated by the writer, and the main results published in this Journal. The third group also received considerable attention during the above investigation, but a recent study both of the type specimens and additional material has revealed new points of interest, and some of these are given in the present article.

Camptosaurus, Marsh, 1885.

The large Dinosaur described by the writer as *Camptosaurus dispar*, of which a restoration also has recently been published,* is now so well known that it may be taken as a form typical of the group. It is exceeded in size by *Camptosaurus amplus*, Marsh, but there are at least two smaller species of the genus (*C. medius* and *C. nanus*, noticed below). So far as at present known, these species are found in successive deposits of the same general horizon, the smallest below and the largest above.

Camptosaurus amplus is represented by remains which show that this reptile when alive was about thirty feet in length. The type specimen of *C. dispar* was about twenty feet in length, and ten feet in height. *C. medius* was about fifteen feet long. The smallest species of the genus, *C. nanus*, was not more than six feet in length, and perhaps four feet in height when standing at rest. One of the striking features of this diminutive species is its long sigmoid scapula shown in figure 3, Plate V. This is in strong contrast with the short, straight scapula of *C. dispar*, seen on the same plate, figure 2. The limb bones of all the species of this genus are very hollow.

* This Journal, vol. xlvii, p. 245, March, 1894. See also, vol. xviii. p. 501, December, 1879; and vol. xxix, p. 169, February, 1885

The skull, brain, and teeth, of *C. medius* are shown on Plate IV. The peculiar peg and notch articulation in the sacral vertebræ of this genus, already described, is indicated on Plate VI, figure 2, and a summary of the principal characters of the genus, and of the nearest allied genera, will be found in the text below.

Dryosaurus, gen. nov.

Another genus of Jurassic Dinosaurs, allied to *Camptosaurus*, but differing from it in many important respects, is *Dryosaurus*, the one here established. The type was described by the writer in 1878, under the name *Laosaurus altus*, and a tooth, the pelvis, and a hind leg, were also figured.* Additional material since received shows that this genus is quite distinct from *Laosaurus*, to which it was at first referred, and is intermediate between *Camptosaurus* and that genus, as is shown in a summary of the characters of these genera given later in the present article.

The European representative of *Dryosaurus* is *Hypsilophodon*, Huxley, from the Wealden of England. That genus, however, differs from the nearest allied forms of this country in several well-marked characters. Among these, the presence of teeth in the premaxillary bones and a well-ossified sternum are features not seen in American Jurassic forms. The fifth digit of the manus, moreover, in *Hypsilophodon* is almost at right angles to the others, and not nearly parallel with them as in *Dryosaurus*. It agrees with the latter genus in having the tibia longer than the femur.

The only species of *Dryosaurus* at present known is the type first described, and in future this may be called *Dryosaurus altus*. Several specimens of this Dinosaur are preserved in the Yale Museum, and they show it to have been in life about twelve feet long, and one of the most slender and graceful members of the group. The known remains are all from the Atlantosaurus beds of Colorado and Wyoming.

Laosaurus, Marsh, 1878.

The present genus includes several species of diminutive Dinosaurs, all much smaller than those above described, and possessing many features now seen only in existing birds, especially in those of the ostrich family. The two species of the genus first described by the writer (*Laosaurus celer*, the type, and *L. gracilis*)† show these avian features best of all,

* This Journal, vol. xvi, p. 415, plate ix, November, 1878.

† *Ibid.*, vol. xv, p. 244, March, 1878.

and it would be difficult to tell many of the isolated remains from those of birds. A larger species, which may be called *Laosaurus consors*, is now known by several skeletons nearly complete. The type specimen, here figured in part on Plates V–VII, is the most perfect of all, and this was collected by the writer in 1879. The animal when alive was about eight or ten feet in length. The known remains are from the Atlantosaurus beds of Wyoming.

One of the distinctive features of this genus, which separates it at once from those above described, is the pubis. The prepubis, or anterior branch of this bone, which was very large and broad in *Camptosaurus*, still long and spatulate in *Dryosaurus*, is here reduced to a pointed process not much larger than in some birds. These differences are shown in Plate VII, figures 1, 2, and 3.

Nanosaurus, Marsh, 1877.

The smallest known Dinosaur, representing the type species of the present genus, was described by the writer in 1877, under the name *Nanosaurus agilis*.* The type specimen consists of the greater portion of the skull and skeleton of one individual, with the bones more or less displaced, and all entombed in a slab of very hard quartzite. The whole skeleton was probably thus preserved in place, but, before its discovery, a part of the slab had been split off and lost. The remaining portion shows on the split surface many important parts of the skeleton, and these have been further exposed by cutting away the matrix, so that the main characters of the animal can be determined with considerable certainty.

A study of these remains shows that the reptile they represent was one of the typical *Ornithopoda*, and one of the most bird-like yet discovered. A dentary bone in fair preservation (Plate VI, figure 3) indicates that the animal was herbivorous, and the single row of pointed and compressed teeth, thirteen in number and small in size, forms a more regular and uniform series than in any other member of the group. The ilium, also, shown on the same plate, is characteristic of the *Ornithopoda*, having a slender, pointed process in front, but one much shorter than in any of the larger forms. The posterior end is also of moderate size. All the bones of the limbs and feet are extremely hollow, strongly resembling in this respect those of birds. The femur was shorter than the tibia. The metatarsals are greatly elongated and very slender, and there were probably but three functional toes in the hind foot.

* This Journal, vol. xiv, p. 254, September, 1877.

A second form referred by the writer to this genus, under the name *Nanosaurus rex*, may perhaps belong to the genus *Laosaurus*. The femur is shown on Plate VI, figure 5. The animal thus represented was considerably larger than the present type species, and from a somewhat higher horizon in the Atlantosaurus beds.

The type specimen here described, which pertained to an animal about half as large as a domestic fowl, was found in Colorado. This reptile was a contemporary of the carnivorous *Hallopus*, likewise one of the most diminutive of Dinosaurs, and one of the most remarkable.

The various Dinosaurs thus briefly referred to under their respective genera have many other points of interest that cannot be here discussed, but their resemblance to Birds is worthy of some notice. This is apparent in all of them, but, in the diminutive forms, the similarity becomes more striking. In all the latter, the tibia is longer than the femur, a strong, avian character, and one seen in Dinosaurs only in the small bird-like forms.* In *Nanosaurus*, nearly all, if not all, the bones preserved might have pertained to a bird, and the teeth are no evidence against this idea. In the absence of feathers, an anatomist could hardly state positively whether this was a bird-like reptile or a reptilian bird.

The main characters of the four genera above discussed are as follows :—

Camptosaurus.

Premaxillaries edentulous, with horny beak. Teeth large, irregular, and few in number. A supra-orbital fossa. Cervical vertebræ long and opisthocœlous. Lumbars present. Five free vertebræ in sacrum, with peg and notch articulation. Limb bones hollow. Fore limbs small. Sternum unossified. Five functional digits in manus. Prepubis long and broad; postpubis elongated. Femur longer than tibia. Metatarsals short. Three functional digits in pes; the first rudimentary, and the fifth wanting.

Dryosaurus.

Premaxillaries edentulous, with horny beak. Teeth of moderate size. A supra-orbital fossa. Cervicals long and biconcave. No lumbars. Six coössified vertebræ in sacrum, without peg and notch articulation. Limb bones hollow. Fore limbs very small. Sternum unossified. Five digits in manus. Prepubis long and narrow; postpubis elongate and slender. Posterior limbs very long. Femur shorter than tibia. Metatarsals long and hollow. First digit in pes complete; fifth metatarsal represented by short splint only.

*Besides the genera here mentioned, *Cœlurus*, *Compsognathus*, and *Hallopus* also possess this character.

Laosaurus.

Premaxillaries edentulous. Teeth small and irregular. Cervicals short and flat. Six vertebræ in sacrum; no peg and notch articulation. Sternum unossified. Fore limbs small. Limb and foot bones hollow. Prepubis very short and pointed; postpubis slender. Femur shorter than tibia. Metatarsals elongate. First digit in pes functional; fifth rudimentary.

Nanosaurus.

Teeth compressed and pointed, and in a single uniform row. Cervical and dorsal vertebræ short and biconcave. Sacral vertebræ three (?). Anterior caudals short. Ilium with very short, pointed front, and narrow posterior end. Fore limbs of moderate size. Limb bones and others very hollow. Femur curved and shorter than tibia. Fibula pointed below. Metatarsals very long and slender.

The genera thus defined contain all the known forms of the the typical *Ornithopoda* from the American Jurassic. They are, moreover, the earliest representatives of this group known in this country from osseous remains, as such fossils have not yet been found in the Triassic, where the oldest Dinosaurs occur. Some of the bird-like footprints in the Connecticut river sandstone may indeed have been made by Dinosaurs of this group, but there is no positive evidence on this point. The American Cretaceous forms of the typical *Ornithopoda*, so far as at present known, are all of large size, and highly specialized, and this appears to be true, also, of the Old World species.

In considering the relations of this well-marked group, here called the typical *Ornithopoda*, with the other two nearest allied suborders, the quadrupedal *Stegosauria* and *Ceratopsia*, it becomes evident, as previously shown by the writer, that all three belong in one great group, which may be regarded as an order. Although differing widely from each other in many notable features, they have a few characters in common, which are important enough to bind them together, and perhaps to indicate a common origin. The most significant of the characters shared by all is the predentary bone, which no other vertebrates possess. Another common character of importance, although sometimes nearly obsolete, is a postpubic bone which is present in all Birds, although in some recent forms it is rudimentary. A comparative series showing the relative development of the anterior and posterior branches of the pubis in six genera of American Predentate Dinosaurs is shown in Plate VII.

In recognition of the manifest relations of the three groups, *Ornithopoda* as here restricted, *Stegosauria*, and *Ceratopsia*, sharply defined as suborders, they should be placed together in a single order, which may appropriately be named the PREDENTATA. This order should be regarded as of equal rank with the *Sauropoda*, the *Theropoda*, and perhaps also the *Hallopoda*, as defined by the writer, the whole constituting the subclass known as the *Dinosauria*.

Yale University Museum, New Haven, Conn., June 15, 1894.

EXPLANATION OF PLATES.

PLATE IV.

FIGURE 1.—Skull of *Camptosaurus medius*, Marsh; seen from the left side.

FIGURE 2.—The same skull, with brain-cast in position; seen from above. Both figures are one-fourth natural size.

FIGURE 3.—Tenth upper tooth of *Camptosaurus medius*.

FIGURE 4.—Fifth lower tooth of same species. Both figures are natural size. *a*, outer view; *b*, posterior end view; *c*, inner view.

PLATE V.

FIGURE 1.—Pelvis of *Camptosaurus dispar*, Marsh; seen from the left. One-twelfth natural size.

FIGURE 2.—Left fore leg of same species. One-twelfth natural size.

FIGURE 3.—Left fore leg of *Camptosaurus nanus*, Marsh. One-fourth natural size.

FIGURE 4.—Left hind leg of *Laosaurus consors*, Marsh. One-sixth natural size.

PLATE VI.

FIGURE 1.—Lower tooth of *Laosaurus consors*. Natural size. *a*, outer view; *b*, posterior end view; *c*, inner view.

FIGURE 2.—Posterior sacral vertebræ of *Camptosaurus dispar*; showing peg and notch articulation; top view. One-fourth natural size.

FIGURE 3.—Dentary bone of *Nanosaurus agilis*, Marsh; seen from the left.

FIGURE 4.—Ilium of same individual; left side. Both figures are natural size.

FIGURE 5.—Left femur of *Nanosaurus rex*, Marsh. One-half natural size. *a*, front view; *b*, side view; *c*, back view; *d*, proximal end; *e*, distal end.

PLATE VII.

FIGURE 1.—Left pubis of *Laosaurus consors*; outer view. One-fourth natural size.

FIGURE 2.—The same bone of *Dryosaurus altus*, Marsh. One-eighth natural size.

FIGURE 3.—The same of *Camptosaurus dispar*. One-twelfth natural size.

FIGURE 4.—The same of *Triceratops prorsus*, Marsh. One-twentieth natural size.

FIGURE 5.—The same of *Claosaurus annectens*, Marsh. One-sixteenth natural size.

FIGURE 6.—The same of *Stegosaurus ungulatus*, Marsh. One-twelfth natural size. *p*, prepubis; *p'*, postpubis.

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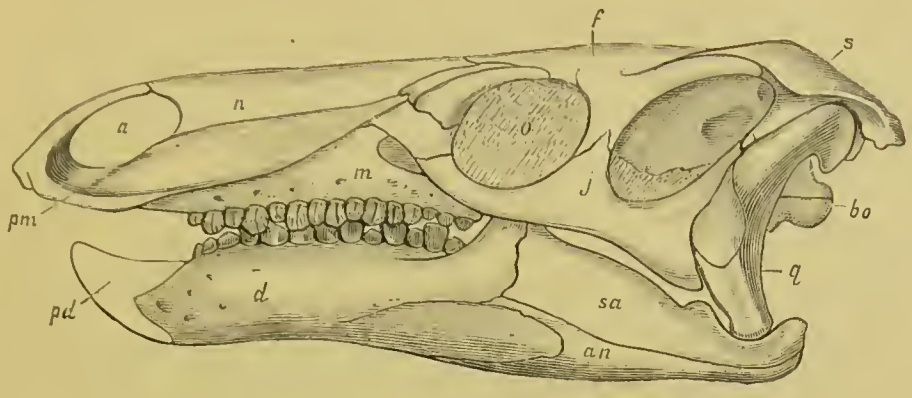

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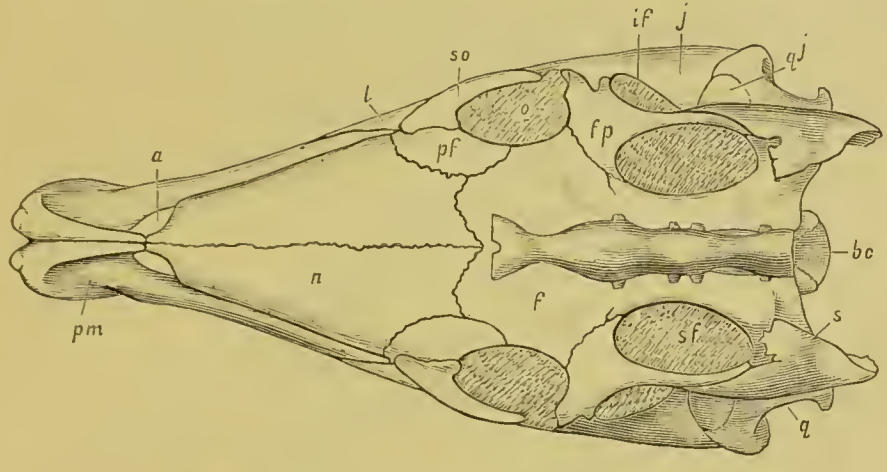

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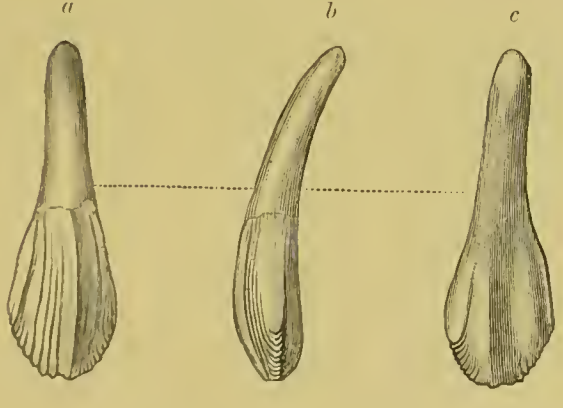

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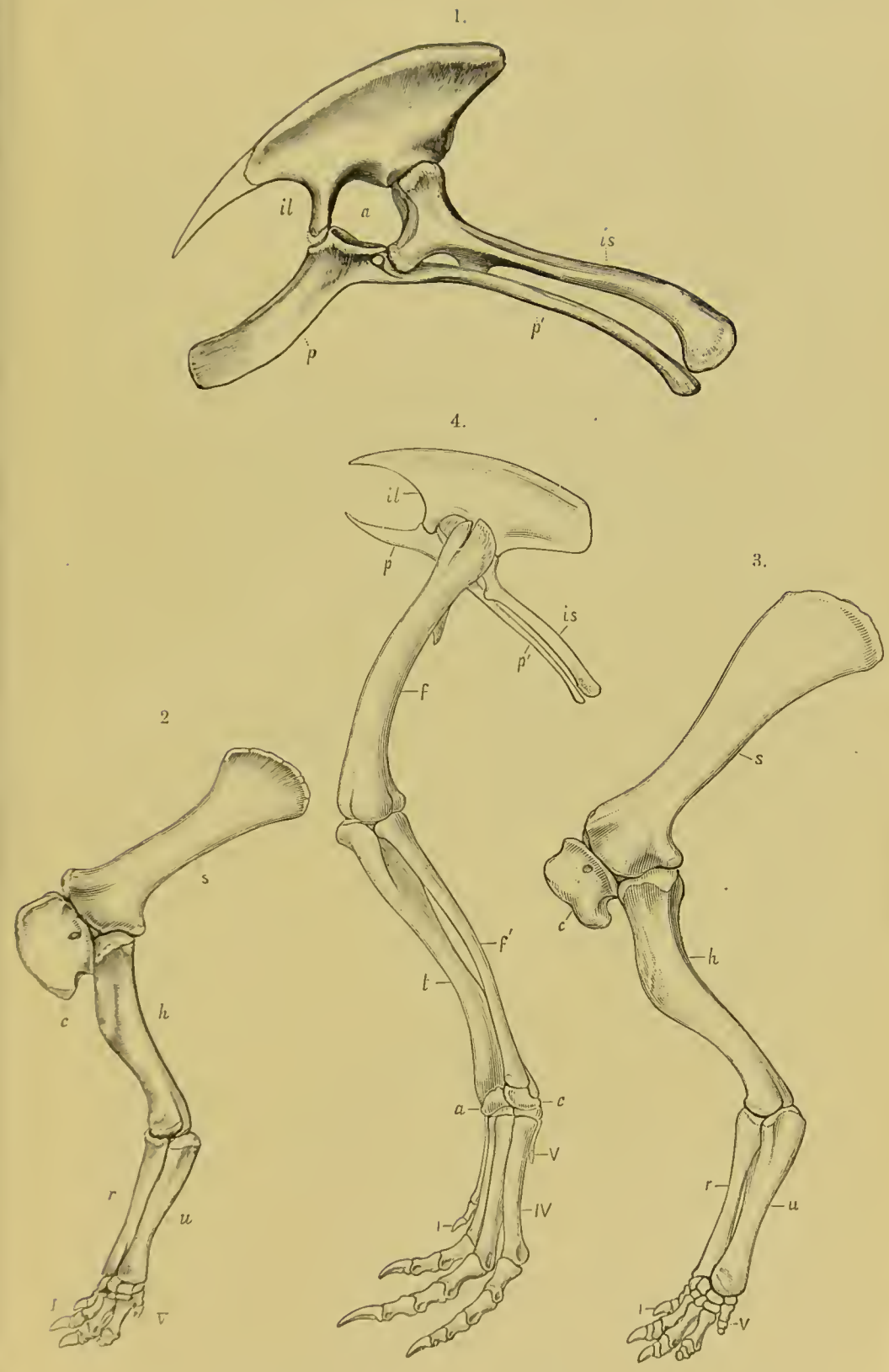
SKULL AND TEETH OF CAMPTOSAURUS MEDIUS, Marsh.



1–3. Camptosaurus. 4. Laosaurus.

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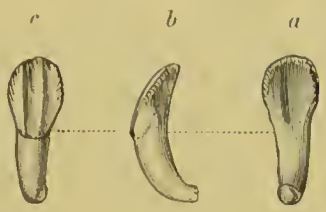

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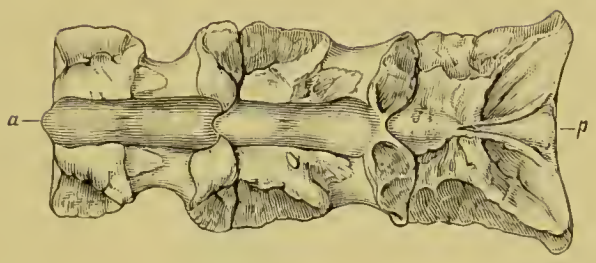

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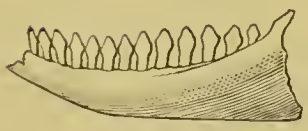

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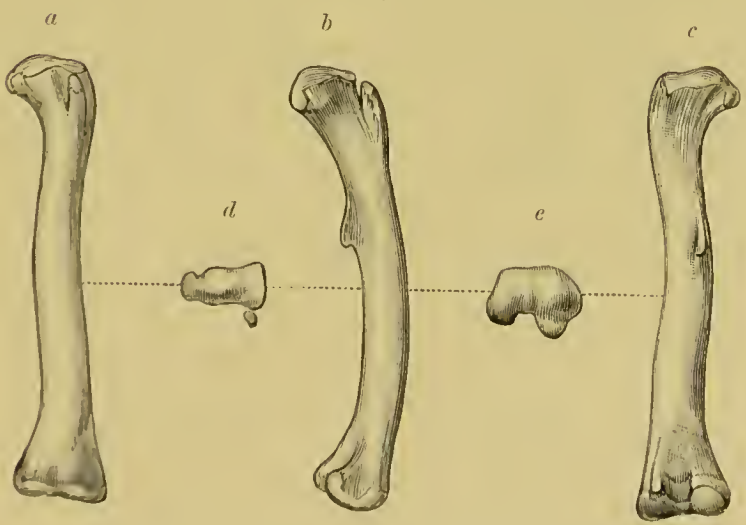

1. Laosaurus. 2. Camptosaurus. 3–5. Nanosaurus.


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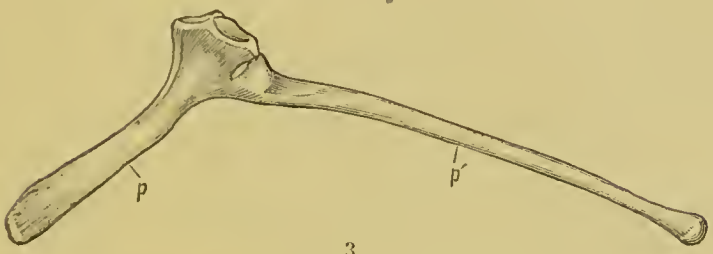

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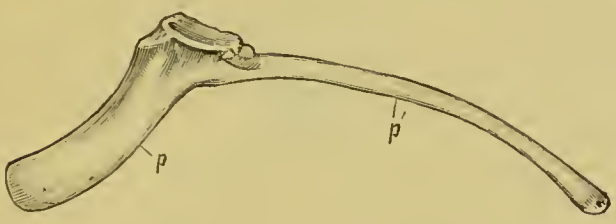

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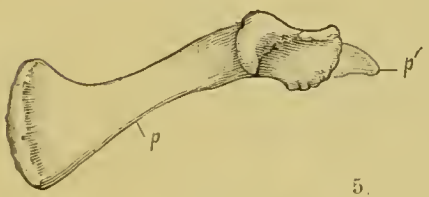

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Pubes of Predentate Dinosauria.


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